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PHENOTYPIC RESPONSE OF *NEOREGELIA JOHANNIS* (BROMELIACEAE) DEPENDENT ON LIGHT INTENSITY REACHING THE PLANT MICROHABITAT

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ABSTRACT. Shoot form varies among many bromeliads according to the light regimes. The authors tested the hypothesis that this type of variation in *Neoregelia johannis* occurs in response to mean amount of light reaching the plant microhabitat and is continuous. The 21 individuals marked in the field included individuals with the most extreme phenotypes available. Leaf length, leaf width, foliar surface, the number, length and width of spines on the leaf border, and the distance between successive spines were measured for each plant, as was the incident light (in lux) at the microhabitat of each plant at one-hour intervals of the day, during different months. Regression analysis was used to test the relationship between light intensity in the microhabitat and each bromeliad morphological variable. Leaf length decreased with the increase of sunlight in the microhabitat, whereas leaf width increased. As the amount of sunlight in the microhabitat increased, spine length and width increased, whereas their number along the border and the distance between adjacent spines diminished. The foliar surface decreased and the ratio leaf width/leaf length increased as exposure increased. The authors conclude that most of the variation in *N. johannis* shoot architecture can be explained by the variation in the light intensity under which each plant grows and that this variation is continuous depending on sunlight received during development.

Many bromeliads show considerable intraspecific variation, especially in shoot size and leaf color. Environmental factors (acting alone or in concert) such as nutrient availability, water supply, temperature and especially light influence vegetative form and pigmentation (Benzing 1980, Medina *et al.* 1986, Lee *et al.* 1989). However, plant responses of this type are usually envisioned as simply biphasic: individuals are capable of expressing either a shade or sun form. A few other investigators (e.g., Lee *et al.* 1989) have suggested or implied potential for graded responses, a possibility that better matches conditions in situ. It seems obvious that, in nature, these plants can grow in a variety of microhabitats in terms of amount of light, that ranges from much attenuated to unfiltered. As a result, a continuous morphological variation rather than a discrete one would seem more plausible.

Neoregelia johannis (Bromeliaceae) occurs abundantly in Atlantic rainforest of Ilha Grande, an island located in the southern of Rio de Janeiro State, Brazil. The bromeliad *N. johannis* is a facultative heliophilous, which in undisturbed Atlantic rainforest occurs only in the top of the canopy and, in secondary Atlantic rainforest, it occurs mainly over rock granite boulders (Almeida 1997). Individual plants at this location experience variable amounts of light and exhibit considerable morphological variation. We hypothesized that the observed variation in the *N. johannis* population is not discrete but matches the gradient of sunlight characteristic of its microsites.

MATERIALS AND METHODS

STUDY AREA. Our study was carried out in an area of secondary Atlantic rainforest near the Village of Vila Dois Rios (23°11′S, 44°12′W) at Ilha Grande, an island in the southern part of Rio de Janeiro State, about 150 km south of Rio de Janeiro City in southeastern Brazil. Ilha Grande is covered by Atlantic rainforest in different stages of regeneration caused by human disturbances during the last centuries. These disturbances ceased when the island, formerly an important area of coffee, corn and sugar plantations, was transformed into a State Park (Araújo & Oliveira 1988). Remnant primary forest (where apparently only selective cuts occurred) persists at the most inaccessible areas of the island. The study was carried out in a secondary forest located at an elevation of 80 m, annual rainfall of ca. 1,700 mm and a mean annual temperature of ca. 23°C.

COLLECTING METHODS AND ANALYSIS. To evaluate if *N. johannis* demonstrates an individual phenotypic response to differences in light intensity in the natural microhabitat, we attempted to sample most of the variations expressed by plants at the study site. In the field we marked

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TABLE 1. Summary of statistics of regression analysis of the different morphological variables of *Neoregelia johannis* as a function of the variation in sunlight intensity reaching the microhabitat of individual plants in the Atlantic rainforest of Ilha Grande, Rio de Janeiro (all results are significant). Letters indicate the regression coefficient (r), the F value (F) and the probability (P).

Phenotypic characteristic	r	F	P
Leaf length (LL)	−0.769	27.530	<0.001
Leaf width (LW)	0.558	8.581	0.009
Distance between spines (DS)	−0.771	27.921	<0.001
Spine length (SL)	0.693	17.579	<0.001
Spine width (SW)	0.553	8.377	0.009
Number of spines on leaf border (NSLB)	−0.697	17.957	<0.001
Leaf surface area (in log) (LSA)	−0.682	16.492	0.001
Ratio leaf width/leaf length (RWL)	0.907	88.250	<0.001

21 adult individuals of *N. johannis* using a numbered plastic band attached to one leaf of each plant. All marks remained throughout the study. We recorded eight variables in three or four leaves for each bromeliad:

i) Leaf length. (to the nearest cm using a measuring tape), the distance from leaf apex to the base of a plant, in four different leaves;
ii) Leaf width. (to the nearest mm using a caliper) at the mid-point of the leaf length, in four different leaves;
iii) Distance between adjacent spines. (to the nearest 0.1 mm with a caliper) measured in the middle of the leaf in four different leaves of each plant. We measured five distances between spines at each leaf border, totaling 10 measures for each leaf;
iv) Spine length. (to the nearest 0.1 mm);
v) Spine width. (to the nearest 0.1 mm) measured at its base. We measured one spine per leaf located at the mid-point of the leaf length, in four different leaves;
vi) Spines on the leaf border. We counted the number of spines along the leaf border at one of the borders of three leaves of each plant. The mean number of spines (MNS) per plant was expressed as the mean number of spines found in the three sampled leaves;
vii) Leaf surface area. (in cm^2), calculated by multiplying leaf length by leaf width; and
viii) Ratio leaf width/leaf length.

Because individuals could be growing during the study, we measured the above morphological variables of each plant at the beginning and at the end of the study. The morphological characteristics of each plant were expressed as the mean of the observed values for each variable in the different leaves measured, at the beginning and at the end of the study.

To estimate the amount of sunlight reaching each plant, we measured incident sunlight at the center of each bromeliad shoot. For this measurement we used a luxmeter (to the nearest 1 lux). To better express the amount of light reaching each individual bromeliad (i.e., its microhabitat) during the day and in different months and seasons, we measured the incident sunlight reaching each bromeliad at hourly intervals from 08:00 to 12:00 and from 15:00 to 17:00 h, on eight different days. Since the amount of sunlight in a particular microhabitat varies throughout the day, among days and seasons because of the angle of the sun, canopy cover and climatic conditions, we included in the study days with different climatic conditions (rainy, sunny and cloudy days). Also, we repeated this set of measurements from April to September and December/96, which included both the dry and rainy seasons. Light integrated exposures were expressed as mean lux measured during the study to obtain an index of incident light (mean amount of light in the microhabitat or MALM). The effects of the light environment on the measured characteristics were determined by regression analysis (Zar 1984).

RESULTS

The shoot morphology of *Neoregelia johannis* individuals varied strongly according to the amount of light reaching the microhabitat of each plant. The relationship between leaf length and MALM was negative and significant ($r = -0.769$; $F = 27.530$; $P < 0.001$; $N = 21$) (TABLE 1, FIGURE 1). Conversely, the leaf width increased exponentially with the increase of MALM of each individual plant ($r = 0.558$; $F = 8.581$; $P = 0.009$; $N = 21$). The distance between spines diminished as MALM increased ($r = -0.771$; $F = 27.921$; $P < 0.001$; $N = 21$). Conversely, the spine length ($r = 0.693$; $F = 17.579$; $P < 0.001$; $N = 21$) and width ($r = 0.553$; $F = 8.377$; $P = 0.009$; $N = 21$) increased

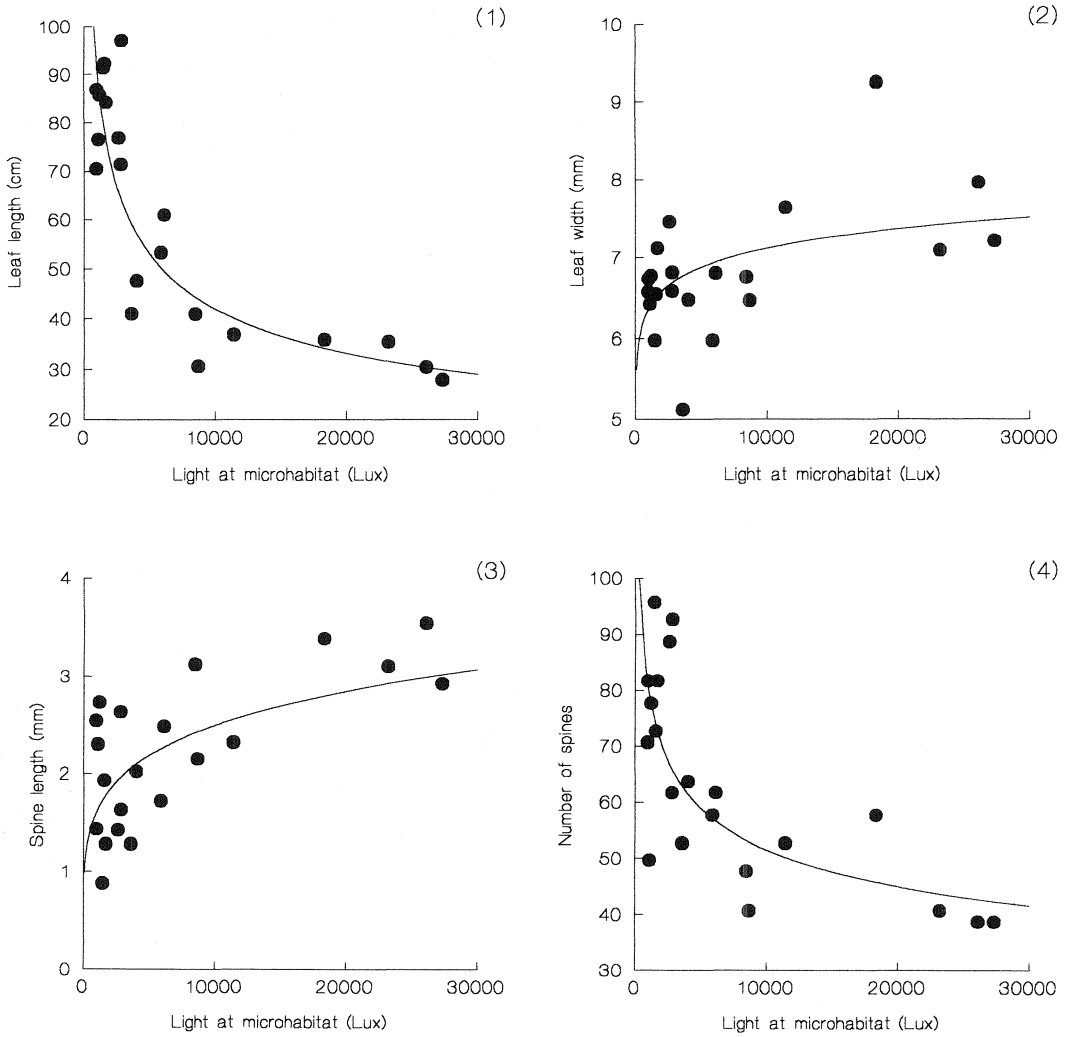

FIGURE 1. Relationship between leaf length (1), leaf width (2), spine length (3) and number of spines (4) and the light ambient experienced by individuals of *Neoregelia johannis* at the study site.

significantly with the increase in MALM. The number of spines along the leaf border decreased with the increase in MALM ($r = -0.697$; $F = 17.957$; $P < 0.001$; $N = 21$). Similarly, the leaf surface area (in log) decreased significantly according to the increase of MALM ($r = -0.682$; $F = 16.492$; $P = 0.001$; $N = 21$). The ratio leaf width/leaf length increased with the increase of MALM ($r = 0.907$; $F = 88.250$; $P < 0.001$; $N = 21$). The color pattern of the individuals also varied markedly with MALM. TABLE 2 summarizes the general characteristics of three easily recognizable phenotypes in the field. Bromeliads living in open-sun have light-green leaves with a conspicuous red semicircle at the leaf apex. In the leaves of some of these individuals, a light green-yellowish coloration occurs. Plants living in relatively shaded microhabitats have dark-green leaves lacking the red semi-circle. *N. johannis* from microhabitats with intermediate MALM developed intermediate green color, sometimes accompanied by the red semicircle (which is in this case usually smaller).

DISCUSSION

The amount of light incident on *N. johannis* affects adult phenotype. Specifically, the amount of light explained much of the variation in many of the measured characteristics. Our data also show that sunlight-induced morphological vari-

TABLE 2. Types of microhabitats and corresponding general sunlight-dependent phenotype developed by individuals of *Neoregelia johannis* in the Atlantic forest area of Ilha Grande, Rio de Janeiro.

Plant microhabitat	Plant phenotype
Sunny microhabitat (18,311 to 27,306 lux)	Plant with relatively short (25–40 cm) and wide leaves (70–95 mm) with comparatively larger and stronger spines relatively less spaced but occurring in smaller numbers. The leaf has a proportionately smaller surface area and a light-green to a light green-yellowish coloration.
Intermediate sunny microhabitat (3,599 to 11,401 lux)	Plant with comparatively intermediate leaf length (40–70 cm) and width (60–75 mm) with thinner and more widely spaced spines occurring in higher numbers than in sunny microhabitat plants. The leaf has a higher surface area than sunny microhabitat plants and an intermediate green coloration.
Shadow microhabitat (939 to 2,839 lux)	Plant with relatively longer (70–100 cm) and narrower leaves (60–70 mm), with small and well spaced spines occurring in larger numbers than the sunny and intermediate sunny microhabitats. The leaf has a large surface area and a dark-green coloration.

ation in *N. johannis* is not discrete (as one can interpret from general literature when authors refers to "sun" and "shade" forms) (e.g., Benzing 1980, Medina *et al.* 1986, Lee *et al.* 1989) but that it is continuous. Our data further indicate that light response is expressed in a diverse set of plant characteristics (leaf length and width, color and surface area, spine length and width, number of spines and distance between them). Incident light is crucial in determining spatial organization (e.g., verticalization) in bromeliad and other epiphyte habitats, because each species grows within a particular range of light intensity (Pittendrigh 1948, Benzing 1980, Ackerman 1986). As a result, morphological or color variation dependent on light conditions are common observations. This variation occurs as a means of better adaptation to particular conditions of sunlight intensity (Benzing 1980, Lee *et al.* 1989, Martin 1994). Our data show that leaves of *N. johannis* living in microhabitats receiving relatively smaller amounts of light are longer and narrower and have a greater surface-area, a darker green coloration, and more spines along leaf borders, which are thinner, smaller and more widely spaced, compared to leaves of bromeliads native to light-rich microhabitats. The increase in length and surface area together with the dark-green tone probably occur as a physiological response to increase both light absorption area and concentration of photosynthetic pigments (chlorophyll). Bromeliads living in relatively shaded microhabitats have a higher chlorophyll content per leaf area as mechanical and physiological responses for physically increasing the light harvesting capacity (Martin 1994, Maxwell *et al.* 1994); while in sun-grown plants, the leaves have a higher concentration of carotenoids (as β-carotene) and anthocyanins that protect them from harmful effects of high light exposure to membrane systems (Benzing 1980, Siefermann-Harms 1987, Lee *et al.* 1989). The heliophile *N. johannis* probably copes with the relative lower amount of light available in some forest microhabitats increasing leaf surface area and concentration of light harvesty pigments. Such morphological responses may allow individuals of this heliophile bromeliad to occupy more shaded microhabitats in the forest. The phenotype developed by the plant could possibly change, however, if the mean amount of light reaching the microhabitat is altered (Benzing 1980, Lee *et al.* 1989).

During the study, we noted that even those bromeliads living in relatively shaded microhabitats received direct sunlight for a period of at least some minutes during the day. For some plant species, the extent to direct sunlight is one of the factors affecting such physiological processes as growth, flowering, or even survival (Benzing 1980, Lee *et al.* 1989, Martin 1994). Extent to direct sunlight could help determine which microhabitats in the forest can sustain *N. johannis* and indicate minimum light requirement (see TABLE 2).

Spines of *N. johannis* growing in sunny microhabitats become larger and thicker resulting in more robust growth. Spines (especially thin-skinned ones) may constitute a mechanical defense against large herbivores, most of which are terrestrial, hence more common on the ground than in the canopy (Benzing 1980, Utley & Burt-Utley 1983). More open habitats (with higher sunlight exposure) may facilitate the access of herbivores that perhaps can more easily find and eat the leaves of bromeliads living in such conditions. If larger and thicker spines are adaptations to protect this bromeliad living in sun-exposed microhabitats from the action of herbivores, the subject deserves further studies.

We conclude that most of the morphological variation of *N. johannis* can be explained by the variation of sunlight intensity under which each plant develops and that the phenotypic response does not occur in a discrete manner but as a continuum of morphotypes, depending on the amount of sunlight reaching the plant. We suggest that such variation constitutes an adaptive response to local environments.

Data from the present study suggests that knowledge of the mean amount of sunlight reaching a given microhabitat allows prediction of the phenotype that an individual will develop as an adult, if light conditions do not change.

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